ify the distribution of the mammals in such a way that without paleontological researches it would be impossible to recognize the origin of the different faunal elements, the fresh-water faunas have resisted almost unchanged all modifications in the configuration of the continent.

The fresh-water fauna is not only older but also much more conservative than the distribution of the mammals. One of the most striking examples of this is given by the history of Africa. While the characteristic mammals are Neogene immigrants and Lydekker proceeds quite correctly in making Africa an annex only of the Holarctic region, thus establishing his Arctogæa, with relation to the fresh-water fauna, Africa is a part of South America, somewhat modified by the Neogene invasion of Cyprinid fishes. If as regards mammals Africa belongs to Arctogæa, with relation to the fresh-water fauna it belongs to the Archhelenic region.

This example demonstrates *the absurdity of the present system of construction of zoogeographical regions and maps. We can construct maps of the different classes and orders but not at all of the animal kingdom, because the geological history of the different groups is quite different.* When Osborn says that it is one problem 'to connect living distribution with distribution of past time,' he says only what had been the leading idea of Wallace and of Engler in their eminent works on zoo- and phytogeography, but when he continues 'and to propose a system which will be in harmony with both sets of facts,' he proposes a problem just as contradictory as would be the construction of descriptions and figures referring at the same time to egg, larva, nympha and imago of an insect. The works on 'zoogeography' are almost exclusively discussions of the distribution of mammals and birds, and the few words spent on other classes are only ornamental supplements. A wrong method cannot give valid results. For the exploration of the zoogeographical relations and regions of the beginning of the Tertiary and of the preceding Mesozoic epoch it is necessary to study and to discuss the more ancient classes and, as I have insisted for ten years, principally the fresh-water fauna.

H. VON IHERING.

SÃO PAULO, July 20, 1900.

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*A HISTORY OF THE DEVELOPMENT OF THE QUANTITATIVE STUDY OF VARIATION.**

THE quantitative study of variation has for its object the investigation of evolution by exact, quantitative methods. The study demands a mathematical method as well as a biological subject matter; consequently the development of the science has proceeded along two main lines—the one biological and the other mathematical. Accordingly, the history of the development of the quantitative method involves a consideration of both the study of variation and the elaboration of the necessary method.

The fact of variation has been recognized since man began to think and to appreciate that in stature, color and mental capacity his fellow-men are diverse. The way for quantitative studies in biology was paved by the mathematical studies on the variation of measurements which engineers and astronomers found it necessary to make for their own purposes. These mathematical studies led to the discovery and elaboration of the law of error by Gauss and others—and this law is the corner-stone of the quantitative biological studies.

The application of the law of error to organic variation was, apparently, first made by an anthropological statistician, of the early part of the century, named Quetelet. In his book, entitled 'Lettres à Son Altesse Royale le Duc de Saxe-Coburg et

* Being part of the report of the Committee of the American Association for the Advancement of Science on the Quantitative Study of Variation.

Gotha sur la théorie des probabilités appliqués aux sciences morales et politiques,' published in Brussels, 1846, and translated into English by O. G. Downes, 1849, Quetelet applied the mean and probable error to the designation of the peculiarities of different races of men; and he even compared an observed distribution of frequencies of human statures with a theoretical one calculated from the mean and the probable error by the use of the formula,

$$y = \frac{2}{\sqrt{\pi}} \int_0^t e^{-t^2} dt.$$

The possibilities of an extension of this method of quantitative analysis to biological variation in general were, however, during twenty years unrecognized, for the time was not yet ripe.

Meanwhile, on the biological side the clouds of a revolution were rising. During the fifties the variation of animals in nature was much discussed. In 1856 Wollaston wrote a book 'On the Variation of Species,' and at a meeting of the British Association, in the same year, Jenyns called for exact data on the variation of organisms. Then came the 'Origin of Species,' 1858, 1859, which used the facts of variation to enforce the conclusion of the mutability of species. At that time the study of the variation of species received a great impetus, but for forty years the observations have been for the most part qualitative or only roughly quantitative. Among the most important synoptic works on variation have been Darwin's 'Variation of Animals and Plants under Domestication,' 1868, and Bateson's 'Materials for the Study of Variation,' 1894.

To the rule that until a decade ago studies in variation were qualitative, the anthropological studies have formed a striking exception. Anthropologists have been forced to measure by the necessity of making fine discriminations, and have sought by statistical methods to get the most out of the resulting data. The first to advance beyond Quetelet was Francis Galton, cousin of Darwin, and already well known on account of his studies on heredity. In 1870, in his book on 'Hereditary Genius,' he used Quetelet's method of applying the law of error to organisms. He used it especially to get a quantitative definition of his grades of ability, A to G. In 1879, Galton made a further and important step. He pointed out that "an assumption which lies at the basis of the well-known law of 'Frequency of Error' (commonly expressed by the formula, $y = k \,.\, e^{-h^2x^2}$) is incorrect in many groups of vital and social phenomena." The assumption which Galton combats is "that errors in excess or in deficiency of the truth are equally probable or conversely, that if two fallible measurements have been made of the same object their mathematical mean is more likely to be the true measurement than any other quantity that can be named." Galton goes on to show that this assumption cannot be justified in vital phenomena; for example, in guesses at a color containing 8 parts of white, we are equally apt to err by selecting one with 16 parts and one with 4 parts, yet the error in one case is twice the error in the second case. Conversely, in two guesses at a mid tint, the most reasonable conclusion is not the arithmetic mean of the two, but the geometric mean. If the guesses are 4 and 16, the most probable value is not $\frac{4+16}{2} = 10$ but $\sqrt{4 \times 16} = 8$; for $4:8::8:16$. Galton then extends this case to biological measures in general and calls for a law of error based on the geometric mean. At his suggestion Mr. Donald McAllister worked out a more general form of the probability curve, applicable to a distribution of frequencies based on geometric error, and obtained the result,

$$y=\frac{1}{x\sqrt{\pi}}h^{-h^2\log.^2x}.$$

At about this time also, the anthropologist Stieda called attention in Germany to the application of the probability methods to anthropological statistics. His paper published in the *Archiv für Anthropologie*, Band XIV., entitled 'Ueber die Anwendung der Wahrscheinlichkeitsrechnung in der anthropologischen Statistik,' 1883, has had great influence in extending the use of the method. In this work the measure of variability is the probable error, here called the 'Oscillations Index.'

During the eighties, Galton, in a remarkable series of papers, developed the quantitative theory of individual variation. In 1885 he introduced a graphic method of determining the probable error, using his 'ogive' or normal curve of distribution of error. In connection with his studies on pedigree peas he developed the theory of the mid-parent, the law of regression of the progeny of extraordinary parents toward mediocrity, and the law of ancestral inheritance, according to which the mid-parent contributes one-half, the mid-grand-parent one-fourth, the mid-great-grand-parent one-eighth, and so on, of the whole heritage. In 1888, Galton made another important step. He obtained a method—somewhat rough, to be sure, because chiefly graphic—for measuring *correlation* between two organs. The measures of one organ, called subject, were taken, the mean found and the measures grouped into classes expressed in terms of the deviation from the mean divided by the probable error of the subject. The average of the corresponding measures of the other organ, called relative, was found, and the deviation of the average from the mean size of the organ was expressed in units of the probable error of the relative. The average (found graphically) of the ratios of the deviation of the relative divided by the deviation of the corresponding subject class gives the correlation-index sought.

The culmination of this epoch-making work of Galton was his 'Natural Inheritance,' 1889, which applied the quantitative methods he had elaborated to the data of human inheritance which he had himself gathered. The book is important, not so much for its new material, for much of the matter had appeared elsewhere, but because it called attention to the possibilities of the quantitative method applied to biology generally. But probably of even greater effect were Galton's personal suggestions to biologists such as Weldon and to mathematicians such as Pearson. At any rate, the beginning of the new decade saw the beginning of a wider interest in the quantitative study of variation; and the source of this wider interest can be traced directly to one man—*Francis Galton*.

While the impetus to the modern quantitative variation studies came from Galton, quantitative studies, in zoology at least, were not unknown before 1890. In our own country, Baird, Coues and J. A. Allen had measured numerous individuals of each of many species of mammals and birds and had published tables of measurements. Allen, in particular, had grasped the importance of the quantitative study of variation, had compared the average dimensions of mammals and birds from different parts of the country and had established* a law of relation between the size of individuals and their distribution which has proved very fertile.

As long ago as 1829, H. Milne-Edwards † gave a table of variations in size of various parts of the body of fourteen individuals of

* J. A. Allen, 'On the Mammals and Winter Birds of East Florida,' etc., Bull. Museum Comparative Zoology at Harvard College, 1871, and 'Geographical Variation among North American Mammals,' Bull. U. S. Geol. and Geog. Survey, Vol. II., 1876.

† *Annales des sciences naturelles* (1), 16, p. 87.

Lacerta muralis. Students of molluscs have also been led in a few instances to quantitative studies. One of the most important of these was that of Bateson, who showed by a series of measurements the gradual change in form of the cardiums on the terraces of an inland sea which is gradually becoming denser.

From 1890 on, the published works in the field we are considering became more numerous and appeared simultaneously in several countries and stimulated from various sources. It was early in this decade, too, that the remarkable series, by Pearson and his pupils, of mathematical contributions to the theory of evolution, began to appear. Since these papers profoundly affected biological work, it will be well to consider them first. We may then consider in turn the English biological school—especially the work of Weldon and his pupils—the continental biological work, and finally that of America.

In 1894 Professor Karl Pearson published the first of his valuable series of papers on the mathematics of evolution, entitled 'On the Dissection of Frequency Curves.' While the primary result of these investigations has as yet proved of no great service, the methods elaborated have formed the basis of all Pearson's later analysis. These methods consisted of the analytical investigation of the frequency curve by reduction to the first to fifth movements about an assumed vertical axis. The root of the mean square error was employed as the best measure of variability and was called the standard deviation.

Pearson's second paper: 'Skew Variation in Homogeneous Material,' 1895, is the basis of the newer quantitative methods. Starting with the recognition of the fact that the vast majority of biological frequency curves are not symmetrical but 'skew,' Pearson undertakes an analysis of distribution curves in general, gets a general formula and concludes that there are five types of curves altogether. These are the normal curve—which is symmetrical and has an infinite range; the symmetrical curve with limited range; the skew curve with range unlimited in both directions, with range limited in both directions, and with range unlimited in one direction and limited in the other. The analysis of skew frequency curves was not entirely new, for it had previously been made by an American, E. L. De Forest, of Connecticut. But Pearson's work, having especially a biological aim, has become generally adopted by biologists. In 1897 there was published, posthumously, an analysis of frequency curves by Fechner; but Fechner's treatment is much clumsier than Pearson's. Within recent years a fresh analysis of skew curves has been made by the English mathematician, Edgeworth in the Philosophical Magazine. Sheppard, too, has contributed methods of analysis of frequency curves. All these will doubtless eventually be of service to biologists.

Pearson's third paper, 1896, was devoted to the theory of correlation, which he placed on an analytical basis. His method of getting the index of correlation was a long one, which Duncker has greatly simplified in his paper published a year ago.

Pearson's fourth paper, published jointly with L. N. G. Filon in 1898, dealt with the probable errors of frequency constants and is of great importance for measuring precisely the degree of unreliability of any result. Pearson's later papers, many of which are published under the uniform title 'Data for the Problem of Evolution in Man,' have elaborated and extended the results of his earlier works.

The results of the last six years, then, have placed the analysis of biological frequency curves at once upon a satisfactory scientific basis. But the limit of improvement in the method of analysis is by no means reached.

Passing now to the biological results, we consider first the work done in England, for it was there, in the home of Galton and Pearson that the new methods found their first application. Of the papers of the new era the first is that of Weldon, 1890, entitled 'The Variations occurring in Certain Decapod Crustaceæ. I. Crangon Vulgaris.' Proceedings of the Royal Society of London, Vol. XLVII, pp. 445–453. This study was undertaken to test Galton's prediction * that selection would not alter the distribution of frequencies in any race. Weldon measured four dimensions in several hundred individuals, calculated the means and probable errors, compared the observed and theoretical frequencies and concluded that Galton's prediction is fully justified. He showed, in addition, that the variation in size of the organs measured occurs with a frequency indicated by the law of error and that the 'probable error' of the same organ is different in different races of the same species.

Next Weldon obtained measurements of the variation of the shrimp *Palæmonetes varians* in Plymouth, which have lately been made the basis of comparison with our American shrimps by Duncker and by Johnson and Hall. These comparisons have established that the otherwise very similar English and American shrimps have modal numbers of rostral spines which are respectively 4 and 8. In 1892 Weldon studied correlative variation in the prawn *Crangon vulgaris* and drew the conclusion that a wide knowledge of the specific constants would give an altogether new kind of knowledge of the physiologic connection between the various organs of animals.

In 1893 Weldon published a fourth paper, on correlated variations in *Carcinus mœnas*, in which he dealt with ratios of various dimensions of the body to the carapace length. It was in these studies that Weldon came across a distribution of frequencies which did not conform with the theoretical distribution, and which Pearson subsequently resolved into two symmetrical curves. Weldon found the coefficient correlations between similar organs in different races to be closely alike.

While Weldon was making these studies, Bateson and Brindley published (1892) their quantitative studies on the length of the forceps of male earwigs, on the length of the cephalic horns of a rhinoceros beetle and on the length of the mandibles and the elytra of a stag beetle. In the first two cases there was a marked discontinuity in the variations. Thus the forceps had modes at 3.5 millimeters and 7 millimeters, and the horns had modes at 4 and 9.5 millimeters. In 1895 Bateson gave statistics of the marvelous variation in color of a chrysomelid beetle, but the data hardly admitted of exact quantitative analysis.

In 1895, Weldon presented to the Royal Society his first report of the committee for conducting statistical inquiries into the measurable characteristics of plants and animals. In this report he gives the results of studies on selective destruction of the rock crab. The climax of the studies of Weldon and his pupil, Thompson, on the rock crab is his presidential address before the British Association (1898) in which he showed that the proportional size of the frontal margin of the crab's carapace had at Plymouth, during the preceding five years, diminished five per cent. Consequently he has been able by means of the quantitative method to measure a real evolutionary change. Moreover, he has been able to put his finger on the cause of this change, for he showed that the silting up of the harbor of Plymouth, and the greater quantity of mud in the harbor, tends to kill off the crabs with broad gill-openings and to let survive only those with narrow gill-openings and a narrow gill (or frontal)

* Natural Inheritance, pp. 119–124.

margin. The expectation, then, that quantitative studies would quickly demonstrate that evolution is going on rapidly in certain instances to-day has been realized.

Another of Weldon's pupils, Warren, has provided statistical data on variation in the crab *Portunus*, and on the variation of ancient, barbarous races as compared with modern civilized ones. More recently he has measured quantitatively the effects on the little crustacean *Daphnia* of various external conditions. Vernon, likewise, has given quantitative data on the effects of external conditions on the development of echinoid larvæ and on echinoid hybrids. Finally, the recent confirmation by Galton of his law of Ancestral Inheritance demands brief mention.

The continental school of variation students includes chiefly botanists. Very early (1887) F. Ludwig, of Greiz, began to make quantitative studies on the variation in the number of ray flowers of the white daisy. These studies he continued and extended to other species, and has published the results in a series of papers appearing in the *Botanisches Centralblatt* from 1895 to the present time. He finds that the variation curves of plants are more frequently multimodal than are those of animals. Ludwig has published two comprehensive papers, in 1898 and 1900 respectively, which have served to extend a knowledge of the new method. At Amsterdam, de Vries has applied statistics to his experimental, chiefly *selective*, plant breeding. He has produced new races of certain very variable species within two to four years. Verschaffelt, a student of de Vries, did good service in calling attention to the importance of the coefficient of variation (or the index of variation divided by the average) for comparative purposes. Verschaffelt also suggested an ingenious measure of skewness, which is very simple but has been largely replaced by Pearson's index. Important work has also been done by L. MacLeod, of Ghent, Belgium, and his pupils, in papers published in Dutch in the *Botanish Jahrboek*.

Among the continental zoologists Heincke was the first in the field. He has applied statistics especially to questions relating to the existence of local races of fishes, and especially the herring. George Duncker, a student of fishes, has been occupied with biological statistics since the early part of the decade. He has written an excellent general treatise on the subject, (1899) in which the more important methods of Pearson are simplified and thus made more generally available. In Italy, Camerano has made a beginning with the quantitative methods.

In America quantitative studies of human variation have been made by anthropologists incited by the work of Galton. Prominent among these are Bowditch, Porter and Boaz. Minot also has made use of Galton's methods. Within late years Bumpus (1897–1899) has applied Galton's methods to variation of *Necturus*, and to the problem of the relation of variation to environment and to selection. Eigenmann and his student, Moenkhaus, have given data on the differences in the *mode* of certain fish characters in successive years and in different environments. The writer and his pupils, Blankinship, Brewster, Bullard and Field, have contributed certain quantitative data upon some of Darwin's laws of variation and upon correlation. The writer has also published a small book on the newer methods which, containing the principal formulæ and tables for calculating curve constants, it is hoped may be found useful by students of the new methods.

To sum up, the quantitative study of biology, the modern impulse to which we owe to Galton, has been furnished with good methods by Pearson. Already the application of these methods has borne fruit in our knowledge of the types of bio-

logical frequency curves, and their change with changing place and environment. The idea of correlation has received a precise definition. The results of experimentation have been quantitatively expressed. The rôle of natural selection, the method of evolution and the laws of inheritance are being discovered. Already we are able to predict greater results from the quantitative method in biology, especially where combined with experimentation, than any which have yet appeared.

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PLANT GEOGRAPHY OF NORTH AMERICA.

COMPOSITION OF THE ROCKY MOUNTAIN FLORA.

IN Southern Wyoming the Great Plains extend across the continental divide, making a break in the Rocky Mountain chain, and dividing it into two groups, the Southern and the Northern Rockies. The former are for the greater part in the State of Colorado, but extend into northern New Mexico as well as southern Wyoming. The Wasatch and Uintah Mountains, although separated from the main claim by the Green River Basin, may also be noted here.*

The Northern Rockies begin in northern Wyoming, but have their best development in western Montana, northern Idaho, western Alberta and eastern British Columbia. The chain also extends into Alaska and Yukon Territory, but the flora of this region is partly very little known and so merged into the Pacific Coast flora that it deserves a separate treatment. Some isolated mountains, as for instance the Black Hills of South Dakota and the Little Rockies and Bear Paw Mountains of Montana, may also be mentioned here.

*The mountains of southern New Mexico and Arizona may also be accounted to the Rocky Mountain system, but their flora is so different and contains so many Mexican and Sonoran elements that it is better to exclude them from this discussion.

The flora of the two groups is essentially the same, but some differences are found. These are most evident in the coniferous vegetation. So are for instance *Pinus edulis*, *Pinus aristata*, *Picea Parryana* and *Abies concolor* confined to the Southern Rockies, while *Pinus Murrayana*, *Picea Columbiana* and *Abies grandis* take their place in the Northern. *Psudotsuga mucronata*, *Picea Engelmannii* and *Pinus flexilis* are equally common in both regions.

The flora of the mountain regions is made up of the following elements:

1. The ENDEMIC FLORA OF THE ROCKIES, which constitutes the largest element. In Montana it is represented by 33 per cent. of all the species and in the Southern Rockies the proportion is much larger.

2. The TRANSCONTINENTAL FLORA, made up mostly of hydrophilous plants.

3. The BOREAL FLORA OF NORTH AMERICA, which in British America is more or less transcontinental, but in the United States is found principally in the mountain regions. It is made up mostly of hylophilous plants, but also represented by some hydrophilous ones, as for instance members of *Cyperaceæ*, *Salicaceæ* and *Ericaceæ*.

4. The ARCTIC FLORA, found only on the tops of the highest peaks at an altitude of over 3,000 m. in Montana and over 4,000 m. in southern Colorado.

5. The CASCADE MOUNTAIN FLORA, which merges with that of the Rockies in British Columbia and partly extends south into Montana and Idaho.

But in discussing the flora of the Rockies, one must not only take in consideration that of the mountain regions, but also that of the intermingling plains, valleys and foothills. If this is done, several new elements must also be considered.

6. The FLORA OF THE GREAT PLAINS. The Great Plains consist of high dry tablelands and make up a large portion of Saskatchewan, Assiniboia, eastern Montana